MIOCENE SUIDAE FROM ARRISDRIFT, SOUTH WEST AFRICA–NAMIBIA

By

MARTIN PICKFORD

Institut de Paléontologie, 75005, Paris, France

(With 3 figs and 3 tables)

ABSTRACT

Two taxa of small suids occur at the early middle Miocene locality of Arrisdrift, South West Africa–Namibia. Of these, the more abundantly represented is *Lopholistriodon moruoroti*, a small listriodont previously known from equatorial sites in Kenya. The second, poorly represented species is a small pig with bunodont dentition, possibly related to the subfamily Tetraconodontinae. The relationships of the two species and their implications for biostratigraphy and palaeozoogeography are explored, and it is concluded that the Arrisdrift strata post-date the first of the Neogene Dispersal Phases of Thomas, dated about 17,5 m.y. ago, but that they are unlikely to be as young as 14 m.y. old.

CONTENTS

INTRODUCTION

Arrisdrift, a locality near the Orange River in South West Africa–Namibia, is the only known middle Miocene African fossil locality south of the Nyanza Rift Valley sites of Maboko and Nyakach, Kenya, which occur a few kilometres south of the equator (Pickford 1984). It is evidently somewhat younger, on the basis of its faunal content, than other fossiliferous strata in South West Africa–Namibia (Stromer 1926) at Langental, Elizabethfeld, Bogenfels and Fiskus (Hendey 1984). The distance between the equatorial Kenyan sites and Arrisdrift is more than 3 000 km; yet some of the fossil Suidae from the two regions appear, on the basis of available evidence, to be comparable, which suggests that the two regions were possibly biostratigraphically and ecologically similar.

Corvinus & Hendey (1978) and Hendey (1978, 1984) suggested, on the basis of the aspect of the entire mammalian fauna, that Arrisdrift may be about 16–15 m.y. old, an estimate that seems reasonable. The ruminants and hyracoids indicate an age slightly younger than Maboko and Buluk, Kenya. The latter site has been radiometrically dated to be about 17,2 m.y. (MacDougall & Watkins 1985), while the former is known to be older than 13 m.y. (Bishop *et al.* 1969).

283

Newly discovered strata at Nachola, northern Kenya, have yielded a comparable fauna, dated about 15,5 m.y. old (work in progress). The Arrisdrift faunas are probably older than those from Fort Ternan, Kenya, dated to be about 14 m.y. (Bishop *et al.* 1969) but possibly somewhat younger (work in progress).

There can be little doubt, therefore, that the Arrisdrift fauna is, in a broad sense, early middle Miocene in age, i.e. somewhere between 17,2 and 14 m.y. old. Its importance is very great, providing, as it does, the only glimpse of a middle Miocene terrestrial fauna for virtually the entire subequatorial expanse of Africa. The zoogeographic and biostratigraphic implications of this important site cannot be overstressed. This detailed systematic description of the suid remains from Arrisdrift will hopefully go some way towards augmenting the already valuable data and preliminary interpretations of the mammal fauna of the site.

The fossil suid material includes cranio-dental fragments of a small lophodont species, teeth and mandible fragments of an unidentified bunodont suid, and postcranial bones that, on the basis of their size, could belong to either of the two forms. The material is in the collections of the South African Museum and bears the catalogue prefix SAM–PQ, which is omitted from the accession numbers given in the text.

SYSTEMATIC DESCRIPTION

Family **Suidae** Gray, 1821

Subfamily Listriodontinae Simpson, 1945

Genus *Lopholistriodon* Pickford & Wilkinson, 1975

Type-species: Lopholistriodon kidogosana Pickford & Wilkinson, 1975.

Diagnosis

A genus that differs from other genera of the subfamily by its small size and the extreme development of the transverse crests in the molars and fourth premolars, with the suppression of accessory cusps. The upper premolars possess enlarged cingula and wide cingular platforms. The nasal ridge is narrow. (After Pickford 1986.)

Lopholistriodon moruoroti Wilkinson, 1976

Figs 1, 2A–C, 3D

Listriodon sp. Harris & Watkins, 1974: 576–577.
Lopholistriodon sp. D Pickford & Wilkinson, 1975: 133.
Lopholistriodon moruoroti Wilkinson, 1976: 242–245, pl. 9 (fig. B). Hendey, 1978: 23. Pickford, 1986: 56–58.

Diagnosis

A small species of *Lopholistriodon* in which the diastemata are rather short, P^1 immediately behind $\underline{C}$, P^2 separated from P^1. Hypoconid crests better developed than in *L. kidogosana*.

Holotype

KNM–MO 5, mandible with roots of left I_{1-3}, complete C_1, P_{3-4}, and M_{1-3}; right I_{1-2}, root I_3, complete C_1, P_2–M_3 (Wilkinson 1976, pl. 9 (fig. B)), housed in the Kenya National Museum, Nairobi, Kenya.

Horizon

Early middle Miocene, possibly about 16 million years.

Type locality

Moruorot, Kenya.

Distribution

Moruorot, Buluk and Maboko, Kenya; Arrisdrift, South West Africa–Namibia.

Material

AD49: upper canine; AD135: left M_3; AD136: left maxilla with P^4–M^3; AD138+316+317: snout with left and right I^1, left I^2, left and right C, and roots of left P^1 and right I^3; AD636: left M_3; AD769: lower molar fragment; AD990: upper canine; AD1727: right I_2; AD1753: left M^2; AD2196: right M_3 broken, in mandible fragment; AD2411: left M^1; AD2535: mesial part of right dM_4; AD2565: left M^1 and broken M^2; AD2658: left dM_4 in mandible fragment; AD2692: distal portion of right M_3; AD2927: right M_3 and distal part of M_2 in mandible fragment; AD3014: right upper canine; AD3015: right I_2; AD3276: distal portion of right dM_4.

Description

Fossil listriodont material from Arrisdrift consists of at least 21 cranio-dental fragments, which can confidently be assigned to a small lophodont pig species that was identified by Hendey (1978) as *Lopholistriodon moruoroti*. In addition there are five postcranial fragments that may belong to this species (see separate section in which the postcranial elements are described).

The Arrisdrift specimens include a snout, hitherto not represented among previously described material; the bulk of the sample duplicates existing information.

Snout. AD138 is the only known snout of this species; it can be compared with that of *Lopholistriodon kidogosana* from Ngorora, Kenya. The Arrisdrift specimen is crushed and warped (Fig. 1A–D) but details of its anatomy can be discerned reasonably satisfactorily. The nasal bones are broken anteriorly but are wide and stout. The premaxilla is slightly spatulate in palatal view, the area in front of the I^3–$\underline{C}$ diastema being wider than the width at the diastema. The roots of the central incisors are widely separated although the mesial edges of the crowns met mesially in life. The roots of I^{1-3} are close together.
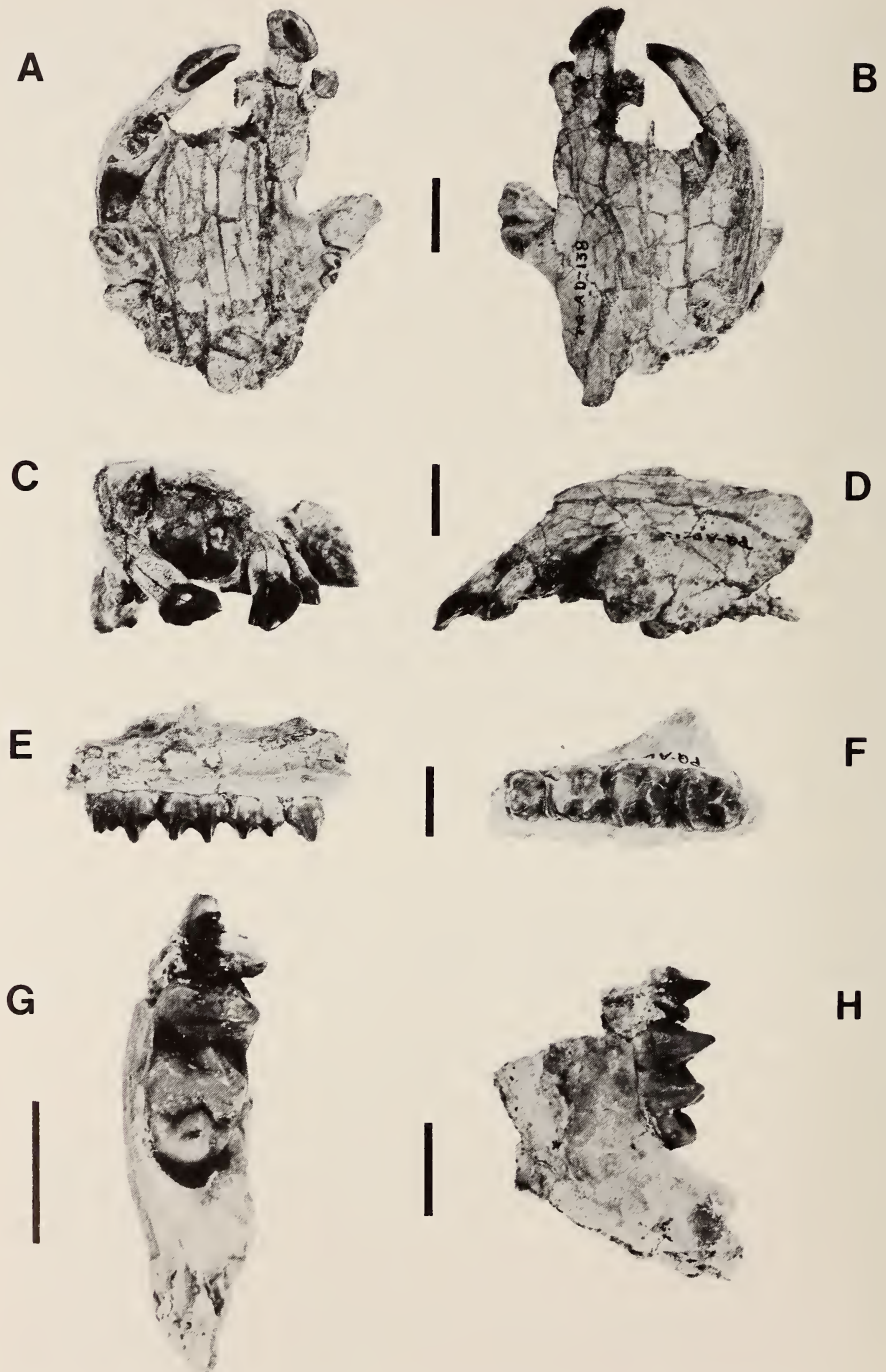
Fig. 1. *Lopholistriodon moruoroti*. A–D. SAM–PQ–AD138: snout with left and right I^1, left I^2, both canines, and roots of left P^1. A. Occlusal view. B. Dorsal view. C. Anterior view. D. Left lateral view. E–F. SAM–PQ–AD136: left maxilla with P^4–M^3. E. Lingual view. F. Occlusal view. G–H. SAM–PQ–AD2927: right mandible fragment with part of M_2 and complete M_3. G. Occlusal view. H. Lingual view. Scales = 1 cm.

TABLE 1

Dimensions (in mm) of the teeth of *Lopholistriodon moruoroti*.

Teeth	Specimen	Length	Breadth
Upper dentition			
Left I^1	AD316	10,5	4,6
Right I^1	AD316	12,0	4,8
Left I^2	AD317	5,5	3,6
Left C	AD138	10,0	7,8
Right C	AD3014	7,8	5,6
Right C	AD138	10,3	7,2
Right C	AD49	8,7	7,9
Left P^4	AD136	5,5	8,4
Left P^4	Mor	6,8	7,9
Left M^1	AD136	9,5	9,1
Left M^1	AD2411	9,9	9,3
Left M^1	AD2565	9,8	9,1
Left M^1	Mor	9+	8,8
Left M^2	AD2565	—	11,0
Left M^2	AD136	10,7	10,5
Left M^2	AD1753	10,9	10,2
Left M^2	Mor	10,5	10,4
Left M^3	AD136	11,3	10,0
Left M^3	Mor	11,0	10,2
Lower dentition			
Right I_2	AD1727	4,3	3,2
Right I_2	AD3015	—	4,2
Left M_3	AD636	12,5+	8,1
Left M_3	AD135	14,0	8,8
Right M_3	AD2927	15,0	8,2
Right M_3	AD2196	14,0	—
Right M_3	Mor	14,5	8,0
Left dM_4	AD2658	12,1	5,1
Right dM_4	AD3276	—	4,0

The premaxillary diastema that housed the lower canine during occlusion has a sharp-edged dorsal ridge, which reaches upwards and laterally above the upper canine to form a supracanine flange, as in *L. kidogosana*.

The upper canines point antero-laterally and slightly downwards, suggesting the possibility that this individual was a female. The palate between the two canines is rather broken but seems originally to have been quite flat. The P^1 roots are close to the upper canine and there is a substantial ridge forming the alveolar process for P^1. Apart from size, the only major difference from *L. kidogosana* is the presence of P^1 roots close to the upper canines.

The upper dentition. I^1 is well preserved in the snout (AD138). It is mesiodistally elongated with a large lingual cingulum; a lingual fossette above the cingulum is wide and quite deep. The occlusal edge is worn, exposing dentine,

and the pattern of dentine exposure and the wavy labial surface of the enamel suggest that this tooth, when unworn, had terminal pectinations as in *Lopholistriodon kidogosana* and *Listriodon splendens*.

I^1 roots are long and housed in prominent juga, which form the lower lateral parts of the nasal aperture. The roots of I^{2-3}, in contrast, are very small. I^2 is a very small tooth, with a lingual cingulum, a triangular crown in lingual view, with its main wear facet anteriorly situated. The incisive foramina are large and situated in line with the I^2 roots, far forward in the palate.

The canines are closed-rooted, tusk-like teeth tapering from the cervix both crownwards and rootwards. A single large anterior facet is worn by occlusion with the lower canine (Fig. 3D). This facet is almost vertically oriented, and its palato-dorsal dimension is greater than its mesiodistal width.

Maxilla and posterior upper dentition. AD136 is a left maxilla with P^4–M^3 and part of the zygomatic process of the maxilla (Fig. 1E–F). The distal surface of the zygomatic root is opposite M^3 and there is a small projection of maxilla behind M^3. The greater palatine foramen is close to the edge of the palate on a level with the front of M^2.

P^4 is a markedly lophodont tooth, surrounded anteriorly, buccally and . distally by a cingulum. The disto-buccal cusp is greatly reduced, appearing as a slight cusplet on the disto-buccal crest. The molars are all strongly bilophodont, but there are ridges leading into the median valley from both lophs, forming characteristic low antero-posterior crests in the midline of the teeth. All the upper molars bear peripheral cingula.

Mandibles and lower dentition. AD2658 is a juvenile mandible with left dM_4 and part of the symphysis up to the midline (Fig. 2A–B), which indicates that this species had a spatulate symphysis as in the genus *Listriodon*. The dM_4 is comprised of three lophs, the distal loph being the widest. Antero-posterior crests run into the median and distal transverse valleys of the tooth.

AD2927 (Fig. 1G–H) and 2196 are small mandibular fragments each containing M_3. The mandibles are gracile, the roots of M_3 are fused bucco-lingually, and the ascending ramus is well behind M_3 as in *Listriodon* species, in contrast to most other suids, where it hides the rear of M_3 in lateral view.

The lower third molars are comprised of two main lophs, behind which is a well-developed, centrally positioned talonid. The anterior lophs are extremely lophodont, with most of the grooves and crests suppressed, but the median accessory cusp is joined by a well-developed crest to the hypoconid. In the latter respect, this tooth differs from that of *L. kidogosana*, in which the homologous crest is almost completely suppressed. The median valley is deep and U-shaped, and is divided into two portions separated by the median accessory cusp. The talonid is comprised of a single centrally positioned cusp, which is probably an enlarged hypoconulid. On either side of it, mesially and laterally, it has low cingula.

In M_2, which is poorly represented in the Arrisdrift collection (Fig. 1H), the hypoconulid is small and positioned close behind the distal loph.

Fig. 2. A–C. *Lopholistriodon moruoroti*. A–B. SAM–PQ–AD2658: juvenile left mandible (with mirror image) containing dM$_4$. A. Occlusal view. B. Lingual view. C. SAM–P–AD3015: right I$_2$, lingual view.
D–G. Gen. et sp. indet. D–E. SAM–PQ–AD1697: juvenile right mandible (with mirror image) containing dI$_1$–I$_2$. D. Occlusal view. E. Lingual view. F. SAM–PQ–AD102d: left I$_2$, occlusal view. G. SAM–PQ–AD20d: lower central incisor. Scales = 1 cm.

The I$_2$ (AD1727) has a distal scoop typical of listriodonts, bordered centrally by a lingual ridge. It has a very light lingual cingulum, but its crown is appreciably longer from cervix to tip than are the corresponding crowns in *L. kidogosana* or species of *Listriodon* (see Pickford 1986).

Remarks

The listriodont fossils from Arrisdrift, Maboko and Moruorot are morphologically and metrically very similar. There can be little doubt that they should be classified in the same species. What is perhaps more difficult to understand is the phyletic position of *Lopholistriodon moruoroti*. It is one of the most derived listriodonts in terms of the perfection of its lophodonty, yet it seems to be one of the earliest known members of the subfamily. It does possess some primitive features, including the retention of a two-rooted P^1 situated close to the canine, and a short diastema. Its precursors are unknown, and there seems little possibility that it was derived from any of the early Miocene East African suids, which are now quite well known (Pickford 1986). The alternative is that they were derived from a small Eurasian precursor—perhaps one of the *Palaeochoerus*-like suids of the early Miocene of Europe—and that they migrated into Africa about 17,5 m.y. ago at the time when many African taxa were translocating to Europe and Asia (Thomas 1985). However, there are no obvious links in the fossil record.

Whatever the case may be, it seems that *Lopholistriodon* was an immigrant to East Africa and South West Africa–Namibia, since there is no sign of listriodont ancestry in the early Miocene deposits of Africa. The presence of *Lopholistriodon* in a fossil fauna is therefore probably good evidence that one is dealing with strata less than 17,5 m.y. old, i.e. middle Miocene rather than early Miocene.

Lopholistriodon kidogosana is known from upper middle Miocene sites in East Africa—such as Ngorora, Kenya—the youngest specimens being about 11 m.y. old. The genus has not yet been found in the same deposits as *Hipparion*, suggesting that, like the genus *Listriodon*, its range was entirely within the middle Miocene period. As such it is a useful genus for broad biostratigraphic correlations.

<div align="center">

Family Suidae: gen. et sp. indet.

Figs 2D–G, 3A–C

</div>

Material

See Table 2.

Description

Right M^3 (AD1795) has marked lingual and buccal flare, and a simple talon, which is little more than a distal cingulum (Fig. 3A). It has a fairly large anterior cingulum and anterior accessory cusp; its main cusps are close together and possess subdued wrinkling, suggestive of the presence of thick enamel.

TABLE 2

Dimensions (in mm) of bunodont suid teeth (gen. et sp. indet.) from Arrisdrift.

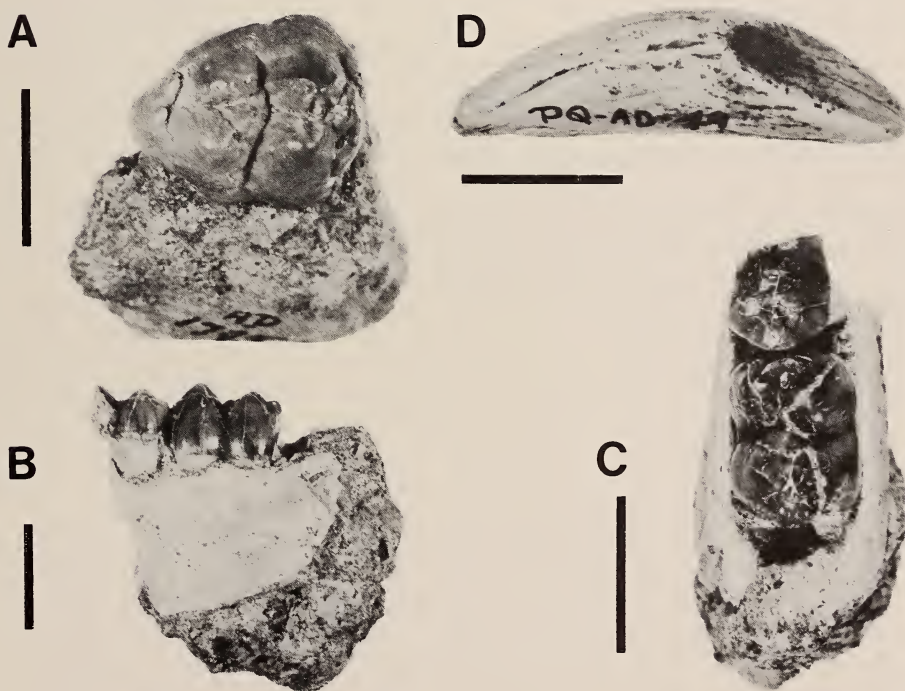| Dentition	Specimen	Length	Breadth
Right M^3	AD1795	16,0	13,1
P^4 fragment	AD2821	—	9,0
Left I_1	AD1693	4,3+	4,8
I_1	AD2355	—	—
Right I_1	AD20d	4,5	4,7
Left I_2	AD102d	4,7	5,0
Left mandible with half dM_4M_1 (M_1)	AD631	11,1	8,9
Right mandible with dI_{1-2} (dI_1)	AD1697	3,1	2,5
(dI_2)		3,4	2,9

Fig. 3. A–C. Gen. et sp. indet. A. SAM–PQ–AD1795: right M^3, occlusal view. B–C. SAM–PQ–AD631: left mandible with half dM_4M_1 (or half M_1–M_2). B. Buccal view. C. Occlusal view. D. *Lopholistriodon moruoroti*. SAM–PQ–AD49: right upper canine. Scales = 1 cm.

AD631 (Fig. 3B–C), a juvenile left mandible with a fragment of M_1 and a complete M_2 (or possibly dM_4–M_1), is comparable to *Nguruwe kijivium* in the morphology of its molar crown, although the tooth is higher crowned than is typical of *Nguruwe*.

AD1697 (Fig. 2D–E) is an infant mandible with dI_{1-2}, and alveoli of dI_3–dM_3. The symphysis, which is complete to the midline, is narrow anteriorly, contrasting with that of *Lopholistriodon*, which is markedly spatulate. The deciduous incisors in the mandible are typically suine, being narrow with concave lingual surfaces bordered by low anterior and posterior ridges. The tip of dI_2 is beaded or crenulated.

AD20d is a rootless, unworn lower central incisor (Fig. 2G), which is pectinate at the tip and which has a central ridge running from crown tip to cervix, as well as mesial and distal lingual ridges.

AD102d is a left I_2 (Fig. 2F), lightly worn with a characteristic distal scoop, lingual rib, and mesial and distal cingular ribs on the lingual side of the crown. The root is long, and in lingual aspect the tooth is gently curved from crown to root, the cervix being more distal than either the root or the crown tips.

Remarks

The eight specimens tentatively assigned to this indeterminate bunodont suid (Table 2) comprise a sample that is insufficient for the purpose of unequivocal identification, bunodonty being a primitive and widespread characteristic of the family. However, the great degree of flare in the upper molars and the lack of buccal and lingual cingula indicate that it is probably not a kubanochoerine, and its affinities possibly lie with genera such as *Palaeochoerus* or *Conohyus*, both of which are well known in Miocene deposits of Europe. More substantial material is required before a positive identification can be made.

POSTCRANIAL BONES

Material

See Table 3.

Remarks

On the basis of their overall sizes, the five postcranial bones from Arrisdrift could belong either to *Lopholistriodon moruoroti* or to the bunodont suid. A decision cannot confidently be made at this time, although—on the basis of quantities of specimens—the chances seem to be higher that they belong to the former rather than the latter. Whatever the final outcome, the available postcranial elements indicate a morphological pattern close to extant suids, from which it is suggested that in its postcranium, the Arrisdrift suid to which these bones belonged was typically suine. Although it was appreciably smaller than any living African suid, the Arrisdrift species was not smaller than the pygmy hog of the Himalaya foothills (*Sus salvinia*).

TABLE 3

Postcranial bones of suid (gen. et sp. indet.) from Arrisdrift (dimensions in mm).

Bone	Specimen	Size
Proximal end left femur	AD3044	
antero-posterior head diameter		15,5
distance from head to greater trochanter		33,3
Complete right tibia	AD2696	
total length		131,2
height of proximal end		22,7
breadth of proximal end		24,5
height of distal end		11,9
breadth of distal end		15,6
Distal end of right tibia	AD646	
height of distal end		11,6
breadth of distal end		15,0
Distal end of metapodial	AD878	
height of distal end		10,5
breadth of distal end		9,5
Distal end of metapodial	AD2711	
height of distal end		9,3
breadth of distal end		8,9

DISCUSSION

The presence of two small suid species at Arrisdrift, in early middle Miocene deposits, is interesting from the point of view of palaeozoogeography, because both may represent immigrants from Eurasia. The subfamily Listriodontinae in particular seems to be absent in lower Miocene deposits of Africa, the only subfamily known in Africa at that time being Kubanochoerinae, which seems to be an unlikely precursor for the listriodonts on a number of morphological grounds (Pickford 1986). On this basis it is suggested that listriodonts migrated into Africa from Eurasia about 17,5 million years ago, and that their origins may be found in the late Oligocene and early Miocene palaeochoerines of Europe.

The bunodont Arrisdrift suid is enigmatic, in that it could represent a peculiar form of kubanochoerine, but I consider it more likely that its affinities lie with the Tetraconodontinae or Palaeochoerinae, both of which are well represented in European deposits of early and middle Miocene age. If this is so then the bunodont Arrisdrift pig would indicate that a second lineage of suids migrated into Africa at the beginning of the early middle Miocene. However, in view of the uncertainty about the identification of this small bunodont pig, it would be unwise to be too dogmatic about this point.

It is probably worth mentioning that isolated teeth have recently been found at Maboko and Nyakach, both of which are early middle Miocene sites in Kenya, which also indicate the probability that Tetraconodontinae were present in Africa

at that time. Unfortunately, none of the specimens is complete enough nor diagnostic enough for the purposes of positive identification, and I prefer to await the discovery of such evidence before using it for biostratigraphic or palaeozoogeographic reconstructions.

Suids often seem to have been in the vanguard of major mammal migrations (Ginsberg, Institut de Paléontologie, Paris, pers. comm.), which makes them interesting for reconstructing the sequence and timing of palaeozoogeographic events. It has been suggested on several occasions (Thomas 1985) that initial crossings of the Tethys Seaway occurred about 19 m.y. ago, a period usually referred to as the 'proboscidean datum'. Suids seem not to have partaken in this particular migration, which has been called the first Neogene Dispersal Phase (NDP 1) by Thomas (1985), but undoubtedly reached Africa before it began, indeed earlier than 20 m.y. ago, since they occur at sites such as Legetet and Songhor in Kenya, and Napak in Uganda, all dated about 20 m.y. Indeed the main groups of mammals implicated in the First Dispersal Phase of Thomas are either very large such as proboscideans, were amphibious such as anthracotheres, or were very small such as rodents and insectivores. This peculiar composition of the migrant fauna suggests that a filter was active in restricting the migrations of medium-sized mammals.

In contrast, numerous medium-sized mammals are implicated in Thomas' second Neogene Dispersal Phase (NDP 2), including bovids, hyracoids, tubulidentates, creodonts and suids. These forms are envisaged as having crossed the Tethys region about 17,5 m.y. ago.

It is probable that, as Africa moved northwards due to plate tectonic processes, it approached close enough to Eurasia about 19 m.y. ago to uplift the floor of the Tethys Sea, making it rather shallow in parts, possibly with islands in certain sectors. At this time, filtered migrations of the first Neogene Dispersal Phase would have been possible. As Africa continued moving northwards, parts of the Tethys sea-floor were elevated above sea-level in continuous strips, effectively providing dry-land crossings from Eurasia to Africa. At this time circulation of sea-water between the Atlantic and Indian oceans through the Tethys was severed, which probably had marked effects on local and global climates. The more pervasive migration of mammals in this second Neogene Dispersal Phase dates this event to about 17,5 m.y. Having migrated from Eurasia into Africa, the suids, particularly *Lopholistriodon*, apparently spread quickly throughout the continent, having been found in early middle Miocene sediments in equatorial and southern Africa.

ACKNOWLEDGEMENTS

REFERENCES

BISHOP, W. W., MILLER, J. A. & FITCH, F. J. 1969. New potassium-argon age determinations relevant to the Miocene fossil mammal sequence in East Africa. *American Journal of Science* **267**: 669–699.

CORVINUS, G. & HENDEY, Q. B. 1978. A new Miocene vertebrate locality at Arrisdrift in Southwest Africa (Namibia). *Neues Jahrbuch für Paläontologie Monatshefte*, Stuttgart **1978** (4): 193–205.

HARRIS, J. M. & WATKINS, R. 1974. New early Miocene vertebrate fauna near Lake Rudolf, Kenya. *Nature*, London **252** (5484): 576–577.

HENDEY, Q. B. 1978. Preliminary report on the Miocene vertebrates from Arrisdrift, South West Africa. *Annals of the South African Museum* **76** (1): 1–41.

HENDEY, Q. B. 1984. Southern African late Tertiary vertebrates. *In:* KLEIN, R. ed. *Southern African prehistory and palaeoenvironments*: 81–106. Rotterdam: Balkema.

MacDOUGALL, I. & WATKINS, R. 1985. Age of hominoid-bearing sequence at Buluk, northern Kenya. *Nature*, London **318** (6042): 175–178.

PICKFORD, M. 1984. Kenya Palaeontology Gazetteer. Volume 1. Western Kenya. *Special Publication National Museums of Kenya*: 1–282.

PICKFORD, M. 1986. A revision of the Miocene Suidae of Africa. *Tertiary Research, Special Paper* **7**: 1–81.

PICKFORD, M. & WILKINSON, A. 1975. Stratigraphic and phylogenetic implications of new Listriodontinae from Kenya. *Netherlands Journal of Zoology* **25** (1): 132–141.

STROMER, E. 1926. Reste Land- und Susswasser-Bewohnender Wirbeltiere aus den Diamant-feldern Deutsch-Sudwestafrika. *In:* KAISER, E. ed. *Die Diamantenwuste Sudwestafrikas* **2**: 107–153. Berlin: D. Reimer.

THOMAS, H. 1985. The lower and middle Miocene land connection of the Afro-Arabian plate and Asia: a major event for hominoid dispersal? *In:* DELSON, E. ed. *Ancestors—the hard evidence*: 42–50. New York: Alan R. Liss.

WILKINSON, A. 1976. The lower Miocene Suidae of Africa. *In:* SAVAGE, R. J. & CORYNDON, S. C. eds. *Fossil vertebrates of Africa* **4**: 173–282. London: Academic Press.